

The University of Chicago

EFFECTS OF SOIL
TEMPERATURE, pH, AND NITROGEN
NUTRITION ON THE DEVELOP-
MENT OF *POA PRATENSIS*

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1937

By

ROBERT A. DARROW

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EFFECTS OF SOIL TEMPERATURE, pH, AND NITROGEN NUTRITION ON THE DEVELOPMENT OF *POA PRATENSIS*¹

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 503

ROBERT A. DARROW

Introduction

Few studies have been made in which plants were grown under the combined influence of controlled nitrogen nutrition, temperature and reaction of the culture medium. In the present series of experiments bluegrass, *Poa pratensis* L., was chosen as a representative plant, sometimes grown in the field under semi-controlled nutrient conditions and differing widely in development with seasonal variation in temperature and soil reaction. The experimental plants were grown with a controlled supply of nitrogen as nitrate or ammonium, under controlled soil temperatures and reaction of the culture media. Measurements of leaf and root growth were taken to express development under the environmental conditions maintained and as a measure of the effects of periodic clipping.

The influence of the reaction of the culture medium on absorption and assimilation of nitrate and ammonium ions has been studied by many workers. NIGHTINGALE (11) has critically reviewed the literature dealing with nitrogen nutrition of green plants, and PARDO (14) reviewed the status of ammonium nutrition. The relation of temperature to nitrogen nutrition has been studied by HARRISON (5) on *Poa pratensis* and by NIGHTINGALE (9, 10, 12, 13) on several plants, including tomatoes, apple trees, and peach trees. Numerous field studies have been conducted on bluegrass, and several greenhouse experiments, notably those by HARRISON (4, 5), AHLGREN (1), GRABER (2), and GRABER and REAM (3), have been concerned with clipping effects.

¹ Supported by a Research Fellowship of the United States Golf Association Green Section.

Experimental data and results

UNCLIPPED SERIES

ELEVEN-WEEKS EXPERIMENT.—To determine the effects of nitrate and ammonium nutrition at varying pH and soil temperatures on the development of unclipped *Poa pratensis* plants, an experiment was set up using the temperature tank apparatus described by LINK (6).

Plants obtained by vegetative propagation from a single plant were grown in 2-gallon crocks filled with acid-washed quartz sand. Two nutrient solutions, one containing nitrogen in the form of nitrate and the second in the form of ammonium, were made up in the usual manner, according to the concentrations outlined in table 1.

TABLE 1
COMPOSITION OF NUTRIENT SOLUTIONS (PARTIAL VOLUME MOLECULAR
CONCENTRATIONS OF SALTS USED)

SOLUTION	KH ₂ PO ₄	Ca(NO ₃) ₂	MgSO ₄	CaCl ₂	(NH ₄) ₂ SO ₄
Nitrate.....	0.00211	0.00286	0.00710		
Ammonium...	0.00211		0.00710	0.00286	0.00286

These concentrations are taken from those of NAFTEL (8). Solutions of three pH values, 4.5, 5.5, and 6.5, were made from each of these stock solutions by the addition of N/10 NaOH or N/10 H₂SO₄ until the desired pH was obtained, colorimetrically measured. The experiment was run in quadruplicate, each of the six nutrient conditions being maintained at three soil temperatures, 15°, 25°, and 35° C. The plants were grown from March 3 to May 10, 1936, under greenhouse conditions and with a relatively large amount of sunshine.

Nutrient solution was added to each culture in 400 cc. amounts twice daily. Regulation of the nutrient medium to the desired pH was accomplished by flushing each culture with distilled water before each nutrient addition. Sufficient water at the desired pH was added to bring the cultures to the proper reaction as determined by testing the leachate colorimetrically. In this way the reaction of each culture was regulated twice daily and the change in pH of the nutrient

solution as indicated in table 2 was manifested over a period of ten hours. It will be seen from the table that plants supplied with nitrate nitrogen at three pH values did not appreciably change the

TABLE 2
WEEKLY pH READINGS ON CULTURE SOLUTIONS CONTAINING PLANTS
GROWN FOR 11 WEEKS IN SAND AT THREE SOIL TEMPERATURES
AND NITRATE AND AMMONIUM NUTRITION AT VARIED pH

No. OF WEEKS	15° C.			25° C.			35° C.		
	4.5	5.5	6.5	4.5	5.5	6.5	4.5	5.5	6.5
NITRATE									
1.....	5.0	5.4	6.4	5.0	5.5	6.5	5.0	5.7	6.5
2.....	5.0	5.6	6.4	5.1	5.7	6.4	5.1	5.8	6.4
3.....	5.1	5.7	6.6	5.1	5.6	6.2	5.2	5.8	6.5
4.....	5.0	5.8	6.6	5.0	5.6	6.2	5.1	5.6	6.4
5.....	5.1	5.7	6.5	5.0	5.4	6.0	5.1	5.5	6.2
6.....	5.0	5.5	6.6	4.0	5.3	6.5	5.0	5.6	5.4
7.....	5.0	5.5	6.5	5.0	5.4	6.3	5.0	5.6	6.2
8.....	4.8	5.6	6.4	4.6	5.4	6.5	5.0	5.6	6.3
9.....	5.0	5.5	5.8	5.0	5.0	6.2	5.0	5.6	6.2
10.....	5.8	5.4	6.2	5.0	5.6	6.3	5.0	5.2	6.3
AMMONIUM									
1.....	5.0	5.4	6.4	5.4	5.5	6.5	5.2	5.5	6.5
2.....	5.0	5.6	6.4	5.2	5.8	6.6	5.3	5.8	6.5
3.....	5.4	5.6	6.5	5.3	5.5	6.1	5.3	5.6	6.0
4.....	4.8	5.6	6.6	5.3	5.3	5.2	5.2	5.5	5.2
5.....	5.1	5.5	6.5	5.1	5.3	5.0	5.0	5.2	4.6
6.....	5.0	5.5	6.5	4.8	5.1	5.6	5.0	5.3	5.0
7.....	4.8	5.5	6.3	4.6	5.4	5.0	5.0	5.3	4.9
8.....	5.0	5.5	5.8	4.6	5.0	5.3	4.6	5.2	5.0
9.....	5.0	5.5	5.4	4.7	5.2	5.3	4.6	5.4	5.0
10.....	5.0	5.2	5.0	5.0	5.0	5.6	5.0	5.0	5.4

reaction of the culture medium over this half-day period, with the exception of the pH 4.5 solution. In general, both nitrate and ammonium solutions applied at pH 4.5 changed rapidly to pH 5.0 and remained fairly constant at that value. Plants supplied with ammonium at pH 6.5 brought about a decided increase in hydrogen ion concentration of the medium, especially at the higher temperatures.

Some increase was noted in the case of solutions supplied at a pH of 5.5.

Measurements were taken for each culture of the length and number of leaves, green and dry weights of roots and leaves, and the number of rhizomes produced. These data are given in tables 3 and 4. Table 3 shows the decided superiority of growth, as evi-

TABLE 3

LEAF AND RHIZOME DEVELOPMENT OF PLANTS GROWN FOR 11 WEEKS IN SAND AT THREE SOIL TEMPERATURES AND NITRATE AND AMMONIUM NUTRITION AT VARIED PH. AVERAGES BASED UPON FOUR PLANTS

TEMPERATURE AND PH	PERCENTAGE INCREASE LEAF LENGTH		PERCENTAGE INCREASE LEAF NUMBER		PERCENTAGE LINEAR INCREMENT		No. OF RHIZOMES	
	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄
15° C.								
4.5	198	31	955	85	3048	145	16.5	3.2
5.5	194	54	942	229	2514	408	18.0	2.8
6.5	191	144	1046	524	2847	1434	32.0	7.5
25° C.								
4.5	173	75	600	35	1842	265	28.0	1.0
5.5	233	115	401	148	1585	442	33.0	3.3
6.5	182	192	620	314	1799	1015	38.0	10.7
35° C.								
4.5	140	23	263	0	761	4	28.5	0
5.5	133	55	226	53	801	141	24.3	1.3
6.5	148	66	170	80	589	209	14.5	2.0

denced by increase in leaf length and number of leaves and rhizomes produced, of the nitrate-supplied plants as compared with ammonium-supplied plants under corresponding temperature and pH conditions. The data for linear increment (a combined measure of leaf length and number) show that nitrate-supplied plants produced almost twice as much growth as plants with ammonium nutrition under pH conditions most favorable for ammonium nutrition. Differences in reaction had no appreciable effect on leaf development of nitrate plants at 15° and 25° C. At 35° C., however, a slight increase in the number of leaves and rhizomes of pH 4.5 plants over the other plants at that temperature was noted. Ammonium plants showed

the least increase in length and number of leaves at pH 4.5 and the best development at pH 6.5 under all temperature conditions.

Temperature effects on leaf development were also evident. In all cases the least development occurred under the highest temperature conditions. The greatest number of leaves was produced at 15° C., whereas increase in leaf length was almost equal at 15° and

TABLE 4

GREEN AND DRY WEIGHTS OF PLANTS GROWN FOR 11 WEEKS IN SAND AT THREE SOIL TEMPERATURES AND NITRATE AND AMMONIUM NUTRITION SUPPLIED AT VARIED PH. AVERAGE WEIGHT (IN GRAMS) BASED UPON FOUR PLANTS

TEMPERATURE AND PH	LEAVES				ROOTS			
	GREEN WEIGHT		DRY WEIGHT		GREEN WEIGHT		DRY WEIGHT	
	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄
15° C.								
4.5.....	17.0	1.1	3.40	0.26	12.6	2.4	4.06	0.85
5.5.....	20.5	2.1	3.48	0.58	14.4	3.1	3.96	1.07
6.5.....	20.1	8.1	3.59	1.71	17.0	7.5	4.50	2.65
25° C.								
4.5.....	10.7	1.0	2.58	0.24	14.0	2.3	5.62	0.91
5.5.....	13.8	2.7	3.27	0.88	12.8	3.2	4.25	1.10
6.5.....	13.1	7.5	3.13	1.77	13.5	7.5	4.78	2.00
35° C.								
4.5.....	5.0	0.8	1.62	0.14	7.0	1.6	3.31	0.44
5.5.....	5.0	1.2	1.56	0.27	7.0	1.7	2.91	0.65
6.5.....	3.5	1.9	1.13	0.43	5.0	2.5	2.21	0.87

25° C. If linear increment is used as a growth index, it is seen that greatest growth, in nitrate plants especially, occurred at the lowest temperature, with decided reductions at higher temperatures. No decided tendencies were noted in rhizome production with respect to temperature, although the maximum number in both nitrate and ammonium plants was produced at the median temperature.

Table 4 shows another index of growth under the conditions of the experiment in the form of green and dry weights of the leaves and roots. The decided superiority in growth of nitrate-supplied over ammonium-supplied plants was evident in all cases. Differ-

ences in weight of nitrate plants owing to pH effects were found only at the highest temperature, at which pH 4.5 plants were superior. Ammonium plants produced the greatest amounts of leaves and roots at pH 6.5. With both nitrate and ammonium nutrition, the root and leaf weights of plants grown at 15° and 25° C. were decidedly superior to corresponding plants grown at 35° C.

Examination of the root systems of the nitrate and ammonium plants showed a general similarity when grown at 15° and 25° C. High temperature caused the production of a root system only half the size produced at lower temperatures.

THREE AND SIX WEEKS EXPERIMENTS.—Two additional series were grown in order to furnish information concerning the early development of plants grown under the conditions of the previous experiment. Two plants were grown in each condition of nutrient supply, temperature, and pH. The procedure described in the previous experiment was followed with the exception that duplicate plants were placed in the same container. For the length of time the experiment was conducted, the amount of nutrient added was sufficient for both plants. The two series were planted on April 26, 1936, and nutrient treatments started on May 4 and continued to May 26 and June 12 respectively for the three and six weeks series. The weather conditions during this period were perhaps a little more favorable for plant growth than during the period of the previous eleven weeks experiment, as longer days and clearer weather prevailed.

Determinations of the reaction of the culture solutions were made at weekly intervals and showed essentially the same general trend in pH that prevailed in the previous experiment. At the end of the sixth week of growth, plants supplied with ammonium at pH 6.5 were active enough to convert the culture solution to pH 5.0. Some increase in acidity of the pH 6.5 solution containing nitrate was noted, but in general the nitrate-supplied plants effected little change in the acidity of the culture solutions.

The development of the plants in these two series was followed in the same manner as in the other experiment, and the results for leaf and rhizome production are shown in tables 5 and 6. The type of response to temperature and nutrient supply was similar in these

shorter series to that shown in the eleven weeks experiment. At the end of three weeks, plants supplied with nitrate at pH 6.5 had superior leaf development except under high temperature conditions, but observations at the end of six weeks showed little difference in pH effect. Ammonium plants showed the best leaf and rhizome development at pH 6.5 at all temperatures, and in all cases the de-

TABLE 5

LEAF AND RHIZOME DEVELOPMENT OF PLANTS GROWN FOR THREE WEEKS IN SAND
AT THREE SOIL TEMPERATURES AND NITRATE AND AMMONIUM NUTRITION
SUPPLIED AT VARIED PH. AVERAGES BASED UPON TWO PLANTS

TEMPERATURE AND PH	PERCENTAGE INCREASE LEAF LENGTH		PERCENTAGE INCREASE LEAF NUMBER		PERCENTAGE LINEAR INCREMENT		NO. OF RHIZOMES	
	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄
15° C.								
4.5.....	35	0	73	16	131	16	2.5	0
5.5.....	40	8	99	13	179	12	3.0	0
6.5.....	56	18	112	24	233	47	4.0	0
25° C.								
4.5.....	23	0	90	0	134	0	4.0	0
5.5.....	33	17	94	11	157	30	2.5	1
6.5.....	65	16	107	27	244	50	0	0
35° C.								
4.5.....	20	0	71	0	105	0	0	0
5.5.....	0	0	64	0	64	0	0.5	0
6.5.....	7	0	34	6	46	0	0	0

velopment of nitrate plants was superior to that of ammonium plants under corresponding conditions. Rhizome production was restricted in the ammonium-supplied plants and no significant differences in number of rhizomes as related to pH could be noted in the nitrate plants.

Green and dry weights of both three and six weeks plants were taken and showed generally the same relations as seen in the eleven weeks experiment. Differences in green and dry weights at the various temperatures were small, especially at 35° C., but a tendency prevailed for maximum weight at pH 6.5 in both nitrate and ammonium plants.

The character of the root systems varied with temperature treatment and with the form of nitrogen nutrition. At the lowest temperature the roots were large in diameter, white, and very succulent, whereas at 35° C. the roots were small, light brown, and very finely branched, forming a densely tufted system. The zone of meristematic development and elongation was very short in roots grown

TABLE 6

LEAF AND RHIZOME DEVELOPMENT OF PLANTS GROWN FOR SIX WEEKS IN SAND AT THREE SOIL TEMPERATURES AND NITRATE AND AMMONIUM NUTRITION SUPPLIED AT VARIED PH. AVERAGES BASED UPON TWO PLANTS

TEMPERATURE AND PH	PERCENTAGE INCREASE LEAF LENGTH		PERCENTAGE INCREASE LEAF NUMBER		PERCENTAGE LINEAR INCREMENT		No. OF RHIZOMES	
	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄	NO ₃	NH ₄
15° C.								
4.5.....	90	0	227	118	530	118	18.0	1.5
5.5.....	110	18	304	135	748	179	12.0	2.0
6.5.....	64	50	547	373	937	603	17.5	9.5
25° C.								
4.5.....	100	8	500	71	1049	81	19.0	1.0
5.5.....	150	25	385	47	1118	88	18.0	1.0
6.5.....	136	41	339	272	944	421	18.5	6.0
35° C.								
4.5.....	40	8	219	0	343	8	11.0	0
5.5.....	30	8	332	8	467	12	5.5	0
6.5.....	21	30	109	39	121	81	10.0	0

at high temperatures, as shown by the presence of laterals almost to the tips of the main roots. Limited data on root tip length indicate that the greatest amount of root elongation took place at the lowest temperature.

Little difference could be noted in roots of nitrate plants with respect to pH value of the culture. Ammonium plants, however, at pH values of 4.5 and 5.5 showed a scant development of lateral roots as compared with plants grown at pH 6.5. At all temperatures the secondary laterals on ammonium plants were very short or stunted and discolored for the proximal 5-8 cm. of the newly

developed crown roots. This reduced condition of the laterals was not noted in nitrate plants.

The leaves of plants grown in this series and the former series show marked differences in degree of succulence as influenced by temperature and pH treatment. The leaves of both nitrate and ammonium plants were more succulent at low temperatures than at high ones. Nitrate plants showed little difference with respect to pH value of the culture at any one temperature, but in the case of ammonium-supplied plants, those grown at pH 6.5 were more succulent than plants grown at pH 4.5 or 5.5. This difference in succulence was more marked at 15° than at 35° C.

CLIPPED SERIES

To furnish information more directly applicable to turf production, an additional experiment was initiated involving the clipping of *Poa pratensis* plants under nitrate and ammonium nutrition at a uniform pH and soil temperature. The temperature tank apparatus was again used to maintain the soil temperatures at 25° C., and both nitrate and ammonium nutrition were supplied as in the previous experiments at pH 6.5. Plants were divided into three lots: clipped at 1 inch weekly, at 2 inches weekly, and control. Ten plants were used for each combination of nutrition and clipping height, and the plants were grown under greenhouse conditions from May 30 to September 14, 1936.

Clipping treatments were started on June 26 and made weekly thereafter, and the number of leaves clipped and the dry weights of the clippings were secured. Weekly counts were also taken of the total number of leaves on all clipped and control plants. Table 7 shows the percentage increase in number of green leaves for each week, based on the original number of leaves. The effects of clipping are shown in the decided reduction in the leaf production of the 1 inch series and the slight reduction in the 2 inch series, compared with the controls. Comparison of the check plants in nitrate and ammonium nutrition shows a more rapid production of leaves in ammonium nutrition throughout the experimental period, except during the first two weeks. Nitrate plants clipped at 2 inches produced more leaves than ammonium plants during the first six weeks

of the experiment, but nitrate plants clipped at 1 inch had in general a smaller production of leaves than corresponding ammonium plants throughout the experiment.

Total dry weights of the weekly clippings are shown in table 8. Nitrate-supplied cultures showed consistently higher yields than ammonium plants, although in most cases this difference was not significant. With the exception of a brief initial period in which insect infestation reduced the number of leaves, there was a consistent increase in yield of clippings over the experimental period in

TABLE 7

PERCENTAGE CUMULATIVE INCREASE OF NUMBER OF LEAVES PRODUCED
BY PLANTS GROWN IN SAND WITH NITRATE AND AMMONIUM
NUTRITION UNDER CLIPPED AND UNCLIPPED CONDITIONS

TREATMENT	JULY 11	JULY 18	JULY 25	AUG. 1	AUG. 8	AUG. 15	AUG. 24	SEPT. 1	SEPT. 8	SEPT. 14
Nitrate										
Check.....	10.1	33.5	71.6	92.5	129.7	150.9	181.3	204.3	219.0	243.0
1 inch.....	6.1	18.1	38.6	55.7	70.4	84.5	92.8	101.2	100.3	99.5
2 inches.....	5.0	31.9	61.3	83.4	112.4	135.8	162.9	180.0	192.4	159.6
Ammonium										
Check.....	7.4	27.5	74.2	104.7	136.9	162.1	205.2	260.1	285.0	307.2
1 inch.....	1.9	16.5	37.9	55.4	72.3	95.2	124.2	148.8	157.4	192.7
2 inches.....		19.0	51.1	74.1	104.6	126.8	164.5	186.5	208.8	200.9

both nitrate and ammonium cultures, particularly in the 2 inch clipping series. Comparison of the yields obtained from the 1 inch and 2 inch series shows the 2 inch nitrate plants to have a greater yield than plants cut at 1 inch. At the end of the experiment, nitrate plants cut at 2 inches were producing three times as much as plants kept at a 1 inch height, and the total amount of clippings obtained throughout the experiment from the 2 inch series was double that for the 1 inch plants. Ammonium-supplied plants, on the contrary, produced a greater amount of clippings during the first four weeks of the experiment when kept at a 1 inch height; and during the last six weeks those plants clipped at 2 inches produced a slightly larger yield than 1 inch plants. Total weight of clippings from the 2 inch ammonium plants was only slightly larger than that obtained from the 1 inch plants.

Comparison of root and rhizome production in nitrate and ammonium-supplied plants showed in general the same relationships as in the previous experiments. Nitrate plants produced a greater number of crown roots than ammonium plants although the average length of roots was greater in the case of ammonium plants. The check plants showed the greatest number of roots and rhizomes under both forms of nutrition, and the 1 inch clipping series showed the poorest developed root systems. A greater number of rhizomes was produced under nitrate nutrition than with ammonium nitrogen.

TABLE 8

DRY WEIGHT (GRAMS) OF CLIPPINGS OBTAINED FROM PLANTS GROWN IN SAND WITH NITRATE AND AMMONIUM NUTRITION AND CLIPPED AT 1 INCH AND 2 INCH HEIGHTS AT WEEKLY INTERVALS

TREATMENT	JULY 3	JULY 11	JULY 18	JULY 25	AUG. 1	AUG. 8	AUG. 15	AUG. 24	SEPT. 1	SEPT. 8	SEPT. 14	TO- TAL
Nitrate												
1 inch.	0.362	0.310	0.183	0.283	0.392	0.371	0.504	0.619	0.660	0.463	0.492	4.64
2 inches. . . .	.416	.327	.134	.377	.737	.800	.950	1.499	1.870	1.218	1.002	9.33
Ammonium												
1 inch.	.335	.260	.143	.284	.305	.328	.303	.429	.516	.401	.375	3.70
2 inches. . . .	0.243	0.229	0.116	0.240	0.369	0.348	0.401	0.583	1.096	0.697	0.594	4.92

Discussion

TEMPERATURE RELATIONS

If the factor of temperature is considered apart from the complex of environmental conditions under which the plants were grown, certain relations of development with temperature differences may be established. The character of the top growth varied considerably within the range of soil temperature used. Low temperatures appeared to be the most favorable both for the production of new leaves and growth in length of leaves. The type of growth resulting at 15° C. was bushy, with long, succulent leaves and numerous new leaves produced. Combined measurements of leaf length and number of leaves or linear increment show the optimum growth temperature to be about 15° C. At soil temperatures of 35° C. the plants were short and rigid, many of the leaves remaining erect

when allowed to grow uncut for three months. Bud initiation and leaf production were limited under the high temperature conditions.

Although chemical studies were not made upon the plants grown at various temperatures, the results can be interpreted partially upon the carbohydrate-nitrogen relationships, as has been done by NIGHTINGALE and others (9, 12, 13). Bluegrass plants in the present experiments, as well as those of HARRISON (5), showed the greatest amount of root and top growth at low temperatures. In both nitrate and ammonium nutrition, absorption of nitrogen took place readily enough at low temperatures so that assimilation and synthesis of protein materials resulted in pronounced increases in leaves and leaf length. High temperatures undoubtedly favored more rapid absorption of nitrogen, as indicated by pH changes in the culture solutions, but assimilation probably did not occur so readily because of the decreased carbohydrates resulting from an unfavorable photosynthesis/respiration balance. As TIEDJENS and ROBBINS (19) point out, nitrate and ammonium ions may accumulate in plants which stop active growth so that apparently the bluegrass plants grown at high temperatures were limited more by carbohydrates than by nitrogen. These implications are further borne out by the yields of top growth produced under the different temperatures and by the number of rhizomes put out by the plants. Equal weights of top growth were produced by plants grown at 15° and 25° C., whereas under soil temperatures of 35° C. the lowest weight of tops and smallest number of rhizomes were produced. Many field and greenhouse experiments with bluegrass and other plants have shown the production of rhizomes to be associated with carbohydrate storage. Under the high temperature conditions of the present experiment, carbohydrates were probably utilized in respiration faster than they were being produced, and consequently few reserves in the form of rhizomes could be established.

The character of the root systems produced was also influenced strongly by temperature. At the lowest temperature the roots of bluegrass were large in diameter, succulent, white, and with few scattered laterals, whereas at 35° C. the roots were small, light brown, and very finely branched into a dense tufted system. These observations agree with those of NIGHTINGALE (10) on apple and

peach roots. The character of the root systems seemed to be influenced by the rate of growth and maturation as evidenced by the root tip lengths. High temperatures favored rapid maturation of roots, with consequent production of laterals almost to the extreme tips of the main roots. At low temperatures more rapid elongation occurred before maturation, causing relatively long tips. The entire root systems at 15° and 25° C. were almost twice as deep as those produced at 35° C. Total root growth as measured by dry weight was equal at 15° and 25° C. and the lowest dry weights were produced at the highest temperature. HARRISON (5), working with bluegrass at temperatures of 60°, 80°, and 100° F., found that no new roots were produced with nitrate nitrogen at any of the root temperatures used over a period of two months. Essentially the same results were obtained in the present investigation, as the nitrate plants produced very few new crown roots at any temperature, whereas with ammonium nutrition many new roots were present.

pH RELATIONS

Under controlled nutrient conditions with nitrogen supplied in the form of nitrate, the plants differed in top and root development with varied pH, depending in part upon their age. Plants of the three weeks series showed a slight tendency for superior development at pH 6.5 at temperatures of 15° and 25°, but at 35° C. the pH 6.5 plants were decidedly inferior in linear increment to plants grown at other pH values. After six and eleven weeks growth, plants grown under similar conditions showed no significant differences with pH at the lower temperatures, but at 35° C. plants grown at pH 6.5 were slightly inferior to pH 4.5 and 5.5 plants. Under the conditions of these experiments the range of pH used apparently had little effect upon absorption and assimilation of nitrate nitrogen except at a soil temperature of 35° C. With high temperatures resulting in more active respiration, the carbohydrate reserves in these plants subjected to high temperatures were at a minimum and assimilation of the absorbed nitrogen was governed more closely by pH. Only under these conditions do the present experiments agree with those of other investigators, as for example, SPRAGUE (16), who found that bluegrass supplied with nitrate and a small amount of

ammonium sulphate produced less top growth at pH 6.5 than at pH 4.5. Root development and rhizome production in nitrate cultures were influenced by pH in the same manner as top development. Weight of roots varied little with differences in pH except at 35° C., under which condition the pH 4.5 plants produced a greater weight of roots.

Plants supplied with nitrogen in the form of ammonium at three pH values showed best development in tops, roots, and rhizomes at pH 6.5, throughout periods of three, six, and eleven weeks growth. The pH range chosen for these experiments was probably not sufficient to cover the true optimum pH for ammonium nutrition as indicated by the work of other investigators. PIRSCHLE (15), TIEDJENS (18), and TIEDJENS and ROBBINS (19) have found that high pH values allow rapid absorption and assimilation of ammonium. At low pH values ammonium ions are absorbed but little assimilation occurs, according to TIEDJENS and ROBBINS.

Rhizome production and root development in these ammonium cultures were also greatest at high pH values. Plants grown in ammonium solutions at pH 6.5 had the most extensive development of lateral roots, whereas at pH 4.5 and 5.5 there was a predominance of stunted, knobby laterals, especially near the base of the main laterals. THERON (17) and MEVIUS (7) have noted this character of roots grown in acid solutions, a result here of insufficient nitrogen assimilation for proper root development. Rhizome production, which has been found by others to occur most abundantly in plants with a plentiful supply of carbohydrates, is correlated here with a pH most favorable for ammonium assimilation, as shown by top development. At high pH values, ammonium-supplied bluegrass plants exhibited a greater vegetative condition, which would seemingly indicate a low carbohydrate reserve, facts which are not in accord with increased rhizome production.

Correlations have been found by several investigators between the amount of absorption of nitrate and ammonium ions at different pH levels and changes in the pH value of the culture media. Absorption of ammonium ions from a solution brings about an increase in acidity of the solution owing to accumulation of residual anions. Thus in the case of the bluegrass plants supplied with ammonium

at pH 6.5 it is seen that month-old plants were capable of reducing the pH of the nutrient solution to 5.0 within ten hours. The rate of absorption of ammonium, as indicated by these changes in reaction of the cultures, is governed primarily by the initial pH and secondly by temperature, greatest absorption occurring at the highest temperatures. Nitrate absorption, on the contrary, is generally slower than ammonium absorption, and there being a more equal absorption of nitrate ions and their associated cations little change in pH results. In the present experiments both nitrate and ammonium solutions applied at pH 4.5 underwent an immediate change to pH 5.0. It would seem by the extreme rapidity with which both pH 4.5 solutions changed in reaction and the difficulty encountered in leaching out the cultures to the proper value, that a part of this change in acidity may be attributed to causes other than absorption of ions by the plant roots.

NITROGEN NUTRITION RELATIONS

UNCLIPPED SERIES.—Within the pH range of the experiments, the plants supplied with nitrate nitrogen showed a markedly better development than those supplied with ammonium nitrogen. The top growth of nitrate plants was superior to that of ammonium plants with respect to number and length of leaves produced and in dry weight of leaves. As has been shown under the discussion of pH relations, this superiority of nitrate nutrition over ammonium nutrition in producing an extremely vegetative plant is probably a result of more rapid assimilation of nitrate within the conditions of these experiments. Absorption rates, as inferred by changes in reaction of the culture media, are indicative of a more rapid absorption of ammonium ions than nitrate ions, but actual assimilation of nitrate ions probably occurred more rapidly under the conditions of the experiments. TIEDJENS and ROBBINS (19) indicate that ammonium at high pH values is more available than nitrate, as evidenced by more rapid stem elongation, greater leaf area, and greater succulence in ammonium-supplied plants as contrasted with nitrate plants. The reactions of the culture solutions used in the present study were probably not alkaline enough to produce optimum growth with ammonium, and hence do not show the effects noted on other plants.

Rhizome and root production varied also with the type of nitrogen nutrition. The number of rhizomes per plant was significantly greater in nitrate plants than in ammonium plants, a fact which can be attributed partially to a more favorable carbohydrate balance under nitrate nutrition. HARRISON (5) also noted this difference in rhizome production under the two forms of nitrogen nutrition. Plants supplied with nitrate showed a greater dry weight of roots than corresponding plants supplied with ammonium, although the actual extent of root systems of the two types was similar. Measurements of root tip length showed more rapid elongation in nitrate plant roots at low and medium temperatures than in ammonium plants, but at 35° C. the latter excelled slightly.

CLIPPED SERIES.—The effects of clipping at 1 and 2 inch heights were studied on plants supplied with nitrate and ammonium nutrition at constant pH and temperature conditions. The plants used were transplants of low carbohydrate reserve and were placed under cutting treatment soon after transferral, facts which should be considered in the interpretation of the results obtained.

Weekly clipping yields showed a consistent increase over the eleven weeks experimental period under all conditions, but were more pronounced in the 2 inch clipping series than in the 1 inch plants. The greater yields of the 2 inch plants as compared with 1 inch may be attributed largely to the carbohydrate relations of the plants. With continuous and ample supply of nitrogen there is a pronounced tendency for vegetative growth, utilizing the available carbohydrates. In the two clipping series, the remaining leaves and stems allow a greater amount of carbohydrate to be built up in the 2 inch series, resulting in greater clipping yields. HARRISON (5) conducted a similar greenhouse study on plants supplied with plus and minus nitrate nutrition, and showed the advantages of carbohydrate reserves in minus-nitrate plants in maintaining a sustained yield on clipping to 0.75 inch height, as opposed to a low carbohydrate reserve in plants continuously supplied with nitrogen. His experiment covered approximately the same time interval as the one here reported, but with the slightly lower clipping height maintained by weekly clippings his plus-nitrate plants did not survive the experiment.

Greater yields were obtained from nitrate-supplied plants than from ammonium plants. On the basis of the previous studies over a

range of pH conditions, it may be concluded that nitrogen in the form of nitrate was more readily available even at pH 6.5 than was ammonium nitrogen, under the conditions of these experiments. Thus with a more readily available form of nitrogen, a greater stimulus was given to vegetative growth and yield with nitrate nutrition over the period in which the clipping studies were conducted.

Availability of nitrogen and relative rates of carbohydrate formation are also factors governing the production of new leaves. Weekly observations of increase in number of leaves on clipped plants showed a slightly greater production by nitrate-supplied plants during the first four to six weeks of the experiment, but during the latter part, ammonium plants produced a denser tuft with greater increase in number of leaves. The control plants initiated more leaves than either of the clipped series, and after the first two weeks of the experiment the ammonium-supplied controls showed the more rapid production of new leaves.

Comparison of these results with comparable portions of the previous experiments brings out several discrepancies with regard to optimum nutrition conditions for leaf production. Thus after three weeks duration, nitrate and ammonium plants had produced the same number of leaves in the clipping series controls, whereas in the three weeks experiment from May 4 to May 26, 1936, nitrate plants were decidedly superior. In the first eleven weeks series, nitrate plants showed almost twice as great an increase as ammonium plants, while the nitrate plants of the clipping series checks, grown under the same pH and temperature conditions, had but one-third as much leaf production as nitrate plants of the first series over the same time interval. However, the ammonium-supplied plants of both series showed almost identical production of new leaves during this time interval. These discrepancies may be due in part to the differences in atmospheric temperature conditions over the two experimental periods. As noted from the first experiment, the greatest number of leaves was produced under low soil temperature conditions, and thus the higher air temperatures prevailing during the clipping experiment played some part in reducing the leaf production of the nitrate check plants. The reasons are not clear for the similarity of leaf production of ammonium plants in the two experiments.

The number of rhizomes produced on the clipped plants was much smaller than on the control plants under both forms of nitrogen nutrition, a fact which has been observed by many workers and is correlated with the smaller amount of carbohydrate reserves established under clipped conditions.

Summary

1. A study was made of the effects of variation in soil temperature, pH, nitrogen nutrition, and clipping height on the development of *Poa pratensis* plants grown in sand cultures under greenhouse conditions.

2. Plants grown at temperatures of 15°, 25°, and 35° C. produced at 15° C. a tall, succulent, bushy top growth with many leaves and at 35° C. an erect, non-succulent, short top growth with few leaves. Root systems of low temperature plants were large, white, succulent, and coarsely branched, while roots of high temperature plants were small in diameter, light brown, and densely tufted.

3. Plants grown with ammonium nutrition at varied pH showed best leaf, rhizome, and root development at pH 6.5, whereas nitrate plants showed little difference within a pH range of 4.5 to 6.5.

4. Nitrate plants were superior in leaf, rhizome, and root development to ammonium-supplied plants under the conditions of temperature and pH of the experiment.

5. Plants supplied with nitrate and ammonium nutrition at constant temperature and pH and clipped weekly at 1 and 2 inch heights showed greater yields with nitrate nutrition than with ammonium nutrition. Yields over a period of eleven weeks were greatest with clipping heights of 2 inches.

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